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PAN-NEOTROPICAL GENUS VENADA (HESPERIIDAE: PYRGINAE) IS NOT MONOTYPIC: FOUR NEW SPECIES OCCUR ON ONE VOLCANO IN THE AREA DE CONSERVACIÓN GUANACASTE, COSTA RICA

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ABSTRACT. Between 1995 and 2004, as part of an ongoing macrolepidopteran inventory of the Area de Conservación Guanacaste (ACG), Costa Rica, 327 adults of the hesperiid genus *Venada* were reared from 636 wild-caught caterpillars and pupae. Although *Venada* was thought to be monotypic over its wide range (Mexico to Bolivia), there are four **new species** on Volcán Cacao in the ACG: *Venada nevada*, *V. daneva*, *V. cacao*, and *V. naranja* — all described by **Burns**, using characters of adult facies, male and female genitalia, caterpillar color pattern, and ecologic distribution. These skippers inhabit both rain and cloud forest, but not dry forest. The caterpillars feed on mature leaves of saplings in five genera of Lauraceae: *Beilschmiedia*, *Licaria*, *Nectandra*, *Ocotea*, and *Persea*. Caterpillars of *Ridens* also eat plants in the family Lauraceae, and *Ridens* and *Venada* may be closely related.

Additional key words: caterpillars, foodplants (Lauraceae), genitalia (male and female), parasitoids, taxonomy, variation.

There are far more species of skipper butterflies in the neotropics than current literature suggests. DNA sequencing is not the only way of revealing them. Granted, DNA sequencing as minimal as barcoding (Hebert et al. 2003a, 2003b) indicates even more species in the common and widespread neotropical skipper Astraptes fulgerator (described by Walch in 1775) than does a synthesis of morphologic, ecologic, ethologic, larval dietary, and other nonmolecular data. But the A. fulgerator complex—with at least 10 species in the Area de Conservación Guanacaste (ACG) of northwestern Costa Rica (Hebert et al. 2004)—is somewhat exceptional. In any case, we show with Venada that a nonmolecular approach to detection of cryptic species still works well.

Evans (1952) erected the skipper genus Venada for just one species. Hence some might consider him a splitter. That would be ironic because, at and around the species level, Evans repeatedly lumped (see, for example, Burns 1964, 1994, 2000, Burns & Kendall 1969, Burns & Janzen 2001). Venada recalls Cephise, another of Evans's (1952) pan-neotropical and monotypic skipper genera. Within the last decade, Cephise has mushroomed to 12 species—some sprung from other genera, some new (Burns 1996, Austin & Mielke 2000)—with yet more to come. Here we add four new species to Venada, all of them present on Volcán Cacao in the ACG. Oddly enough, adults of *Venada* and males of those species of *Cephise* that lack tails are superficially similar (compare Figs. 1–16 with Burns 1996:figs. 28, 29, 32–35 and with Austin & Mielke 2000:figs. 1, 2, 5, 6, 27–30, 33–36, 39, 40; and compare images in Janzen & Hallwachs 2005). *Venada* adults and tailless *Cephise* males are sometimes so similar that even skipper specialists have mistaken one for the other. Externally, the peculiar palpi of *Cephise* (Burns 1996:183 and figs. 24–27) at once distinguish these skippers from *Venada*; internally, the genitalia do so (compare Burns 1996:figs. 1–22 with Figs. 17–29).

In both sexes of *Venada*, four honey-colored spots on the forewing—in spaces 1b, 2 (by far the largest), 3, and the cell (second largest)—are in close contact with one another, forming a conspicuous, irregular patch or band from below mid-costa to above the tornus (Figs. 1–16). Males of *Venada* have a costal fold (Figs. 1, 3, 5, 7). Wingspreads of reared individuals range from about 40 to 50 mm, with males averaging a little less than females. Specimens reared in captivity have smaller wingspreads, on average, than those coming from wildfound pupae.

Although Venada is widely distributed, specimens are rare in collections. Adults of Venada are not strictly crepuscular or nocturnal (like those of various species in such other tropical skipper genera as *Bungalotis*, *Dyscophellus*, *Porphyrogenes*, and *Celaenorrhinus*). Three Venada adults were seen flying rapidly in full sun in the middle of a windless day (27 February 2004) at 1100 m elevation on Volcán Cacao.

MATERIALS AND METHODS

For a description of the large and growing ACG, and of the massive caterpillar rearing and inventory program expanding there over the past quarter-century, see Burns and Janzen (2001), Janzen (2004), and Janzen and Hallwachs (2005). Here we analyze rearing records and 327 adult specimens coming from 636 caterpillars and pupae of *Venada* found between 1995 and 2004. No adults have been netted in the ACG, and the three noted above are the only ones seen in the wild. Reared adults have been deposited in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, USA, and at INBio in Costa Rica.

At the ACG, each wild-caught caterpillar gets an individual code in which the last two digits of the year of collection and a unique number for that year embrace the acronym SRNP (Santa Rosa National Park) with hyphens (e.g., 02-SRNP-23364). The code extends to whatever that caterpillar may produce-i.e., pupa, adult, parasitoid(s). These rearing voucher codes started in 1977 at Santa Rosa National Park, which today is Sector Santa Rosa of the ACG. Skipper genitalia dissection codes (e.g., X-5390) constitute an ongoing, X-rated series begun in 1974 at the Museum of Comparative Zoology, Harvard University, and continued at the USNM. Any pinned adult whose abdomen has been removed for KOH-treatment to aid dissection, is cross-coded with the 1-dram vial of glycerol that holds both the dissected genitalia and the abdominal integument.

RESULTS

To promote brevity, comprehension, and comparison, the descriptions of the four ACG species of *Venada* are tabular. The table itself uses shortening devices: sex symbols; FW, HW for forewing, hindwing; and the vertebrate term "cheeks" for a pair of small, more or less triangular, posteroventrolateral areas on the head of the adult (posterior to the bases of the palpi and ventral to the eyes). When wingshape is described as "sexually dimorphic in the usual skipper fashion," the wings of males are noticeably narrower and more pointed than those of conspecific females.

In naming a new genus for the species originally called *Telegonus advena* Mabille (and soon after, *Nascus advena*), Evans (1952) made the anagram *Venada* of the specific name. Now, in a similar spirit, names of two new species of *Venada* are additional anagrams. The name of the third species is that of the volcano on which all four species live. This name, that of the fourth

species, and one of the anagrams relate to color and, by extension, to color characters in the skippers (see Etymology in Table 1). Names of all *Venada* species are three syllables (with an accent on the middle one) and are meant to be euphonious.

DISCUSSION

Variation. Subtle interspecific differences in brown ground color—which are perceptible in series of fresh, reared adults—generally fade with both the wear and tear of living and the passage of time after death.

Of the four subapical, hyaline, white spots that dot the forewing in spaces 6–9 in the genus Venada, the spot in space 7 is the weakest and the least likely to be expressed (Figs. 1–7, 9–14). This subapical spot series may extend into spaces 5 and especially 4 in both sexes (more often females) of V. naranja and in females of V. nevada. Any such extended appearance in V. nevada females involves space 4 but rarely space 5. A spot in space 4 is vertically oriented in V. naranja (Figs. 8, 16) but angled inward from top to bottom in V. nevada (Figs. 2, 10).

The distal dark band on the ventral hindwing of species of *Venada* tends to be outlined distally with pale yellowish scales. This is most evident in *V. nevada*. The pale scaling is often hypertrophied in females of *V. nevada*, especially in space 2 (Fig. 10). On occasion, development is so extreme that an opaque, pale yellow spot appears on the brown hindwing dorsally at the very same position in space 2. This happens in about 15% of 125 *V. nevada* females.

About halfway along the anteroposterior length of the tegumen, a short, curved, middorsal, sclerotized sac projects dorsoposteriad, just over the roof of the tegumen, in three of seven genitalically dissected males of *V. naranja*: X-5055 (00-SRNP-9252), X-5684 (01-SRNP-6992), and X-5703 (00-SRNP-9469). Typically there is no such prominence in males of *Venada* (Figs. 17–24)—or, for that matter, in males of various related genera.

One of 14 genitalically dissected males of *V. nevada* (X-5709 [03-SRNP-4768]) has a tiny secondary cornutus. This is a sclerotized, sharply pointed spine terminating a short side-sac from the slender, membranous vesica that leads to the large, somewhat comb-like primary cornutus. Although a prominent comb-like cornutus occurs in three ACG species of *Venada* (Figs. 18, 20, 22), there is no trace of a cornutus in the seven dissected males of *V. naranja*.

Foodplants. Like the caterpillars of nearly all other pyrgine hesperiids, the caterpillars of *Venada* eat dicotyledonous plants. But they feed almost exclusively on the mature leaves of saplings in five (or more) genera

TABLE 1. New species of Venada reared from wild-caught caterpillars in the Area de Conservación Guanacaste, Costa Ríca.

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| | | finely dentate oval patch with longitudinal central ridge, on dorsal side of | with longitudinal central ridge, on dorsal (or ventral) side of posterior corpus | small spines aligned and radiating in a bilaterally symmetrical pattern, on dorsal side of posterior | wide band of innumerable fine, mostly longitudinally oriented spines encircling posterior end of corpus |
| | Number examined | 11 | 6 | * | 6 |

TABLE 1. New species of Venada (cont.)

| | V. nevada Burns, n. sp. | V. daneva Burns, n. sp. | V. cacao Burns, n. sp. | V. naranja Burns, n. sp. |
|--|---|--|---|---|
| CATERPILLAR | | | | |
| (ultimate instar): Abdominal color pattern | Fig. 30 6 lateral, vertical, yellow stripes on uniform ground | Fig. 31 4 mid-lateral, yellow to orangish, ellipsoid to round spots on uniform ground | | Fig. 33 3 mid-lateral, yellow, round spots on finely white-dotted ground |
| Head | orange ventrolateral eyespots on black ground; rusty tips to dorsal lobes | orange ventrolateral eyespots on black ground; rusty dorsal lobes | no noticeable eyespots; light rusty to pale orange ground | inconspicuous, reddish ventrolateral eyespots; dark rusty ground |
| Collar/Rump | red/red | red/red | black/pale orange | black/dull tannish |
| FOODPLANTS: Cunoniaceae: | | | | |
| Weinmannia wercklei | 3 | | | |
| Lauraceae: | | | | |
| Beilschmiedia pendula | 4 | | | |
| Beilschmiedia 13641 | 38 | | | 1 |
| Beilschmiedia 14011 | 1 | | | |
| Beilschmiedia sp. | | 1 | | |
| Licaria 13499 | 152 | | 1 | 2 |
| Licaria 13886 | 4 | | | |
| Licaria 14999 | 1 | | | |
| Nectandra hihua | 2 | | | |
| Nectandra martinicensis | 4 | | | |
| Nectandra purpurea | 10 | | | |
| Nectandra salicifolia | 4 | | 1 | |
| Nectandra salicina | 4 | | | |
| Nectandra umbrosa | | 1 | | |
| Nectandra 13808 | 3 | | | |
| Ocotea austinii | | | 4 | 19 |
| Ocotea dendrodaphne | | | | 7 |
| Ocotea insularis | 9 | | | 8 |
| Ocotea mollifolia | 1 | 25 | | |
| Ocotea nicaraguensis | 2 | | | |
| Ocotea veraguensis | 74 | | | 2 |
| Ocotea 13582 | 74 | | | |
| Ocotea 13654 | 5 | | | 1 |
| Persea americana (intro.) | | | 2 | 1 |
| Persea schiedeana | | 133 | | |
| Lauraceae 13487 | 3 | | 7 | 14 |
| Lauraceae 14087 | 1 | | | |
| Lauraceae 16677 | 3 | 3 | | |
| Lauraceae 17369 | | 1 | | |
| ELEVATION RANGE: | 375-1460 m | 620-700 m | 1140-1460 m | 950-1460 m |
| LARVAL HABITAT: | foliage of saplings in edge situations from cloud forest to piedmont rainforest | foliage of saplings in heavily shaded understory of old-growth piedmont | foliage of saplings in edge situations in cloud forest | foliage of saplings in edge situations in cloud forest |
| | | rainforest | | |

| | V. nevada Burns, n. sp. | V. daneva Burns, n. sp. | V. cacao Burns, n. sp. | V. naranja Burns, n. sp. |
|--------------------|---|--|---|--|
| HOLOTYPE MALE: | 02-SRNP-23534 Volcán Cacao, 1185 m, ACG, Costa Rica Lat 10.92714 Long -85.46683 | 02-SRNP-20143 Volcán Cacao, 620 m, ACG, Costa Rica Lat 10.87868 Long -85.38963 | 02-SRNP-23364 Volcán Cacao, 1150 m, ACG, Costa Rica Lat 10.92691 Long -85.46822 | 03-5RNP-4740 Volcán Cacao, 1220 m. ACG, Costa Rica Lat 10.92918 Long -85.46426 |
| DEPOSITION: | USNM | USNM | USNM | USNM |
| PARATYPES: | 108 ೆ, 125 ♀ Volcán Cacao, ACG, Costa Rica | 37 ै, 31 ♀ Volcán Cacao, ACG, Costa Rica | 1 ổ, 3 ♀ Volcán Cacao, ACG, Costa Rica | 11 ♂, 7 ♀ Volcán Cacao, ACG, Costa Rica |
| ETYMOLOGY: | anagram; Spanish for snowfall, which relates to white cheeks | anagram; the other species with white cheeks | known only from high on Volcán Cacao; chocolate relates to dark ground colo | Spanish for orange, the distinctive color of wing r fringes and overscaling |

TABLE 1. New species of Venada (cont.)

of the family Lauraceae: Beilschmiedia, Licaria, Nectandra, Ocotea, and Persea (Table 1). Both V. cacao and V. naranja also use the introduced lauraceous plant Persea americana Mill. However, three of 402 caterpillars of V. nevada (the only species of Venada reared in very large numbers) were found eating mature leaves of saplings of Weinmannia wercklei Standl. (Cunoniaceae) on the edges of the same forest in which the caterpillars are usually found feeding on Lauraceae. Venada nevada and V. naranja are more widespread and have more known foodplant species, while V. daneva and V. cacao appear to be using fewer of the species of lauraceous foodplants in their more restricted habitats. Venada is not found in the adjacent ACG dry forest even though Ocotea veraguensis (Meisn.) Mez, a foodplant of both V. nevada and V. naranja on Volcán Cacao, is common there (Janzen & Hallwachs 2005).

Only 10 other skippers occurring in the ACG eat leaves of Lauraceae: the pyrrhopygines *Jonaspyge aesculapus* (Staudinger) and *Jemadia pseudognetus* (Mabille); and the pyrgines *Zera hosta* Evans, two species of *Dyscophellus*, and five species of *Ridens* (Burns & Janzen 2001, Janzen & Hallwachs 2005). *Jonaspyge aesculapus* is noteworthy because, like *V. nevada*, it also eats *W. wercklei*. This pattern suggests similar chemical attractants in unrelated plants to which unrelated species of skippers convergently respond.

In contrast, selection of Lauraceae by *Ridens* and *Venada* probably reflects common ancestry. Although Evans (1952) described both *Ridens* and *Venada* and considered them related, he made them genera 12 and 18 in his *Urbanus* Group of 20 genera. Foodplants, caterpillar color patterns (Janzen & Hallwachs 2005), adult morphology, and mitochondrial DNA sequences of cytochrome c oxidase I suggest that *Ridens* and *Venada* are much closer. The DNA barcodes clearly distinguish the four ACG species of *Venada* from one

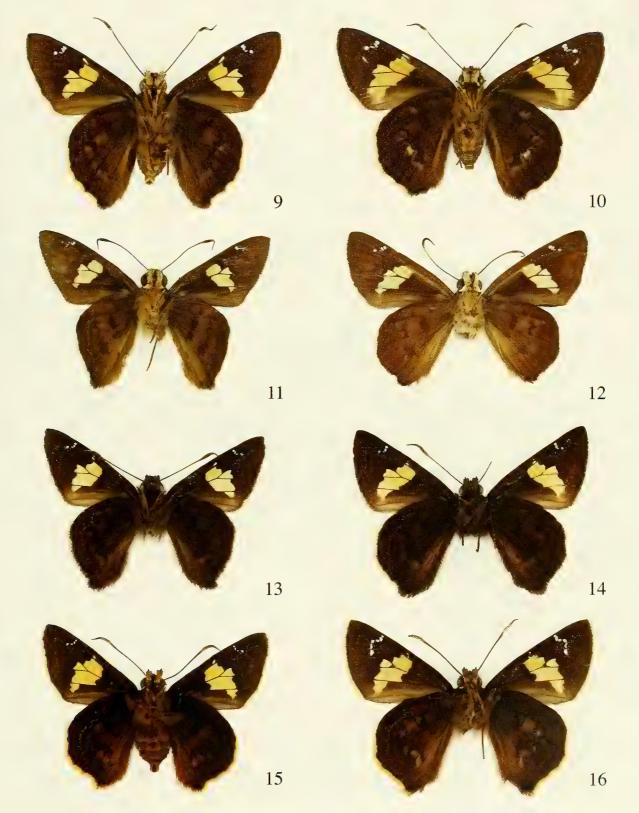
another (Hajibabaei, Hebert, Burns, Janzen & Hallwachs, unpublished). This may be helpful in the future given the superficial similarity of *Venada* adults. (The caterpillars, however, have distinctive color patterns [Figs. 30–33]).

Foodplants of ACG Venada are too limited taxonomically (five genera of Lauraceae) and too shared by these skippers to be of much use in separating them, except in the case of V. daneva whose specific foodplant choices are almost unique (Table 1). The antithesis is the Astraptes fulgerator complex, most of whose 10 ACG species are defined by their disparate larval foodplants-chiefly in the families Sterculiaceae, Malvaceae. Ulmaceae. Fabaceae, Rhamnaceae, Sapindaceae, and Trigoniaceae (Hebert et al. 2004). On the other hand, male and female genitalia do not vary significantly among species of the A. fulgerator complex but clearly distinguish the species of Venada (Figs. 17-29).

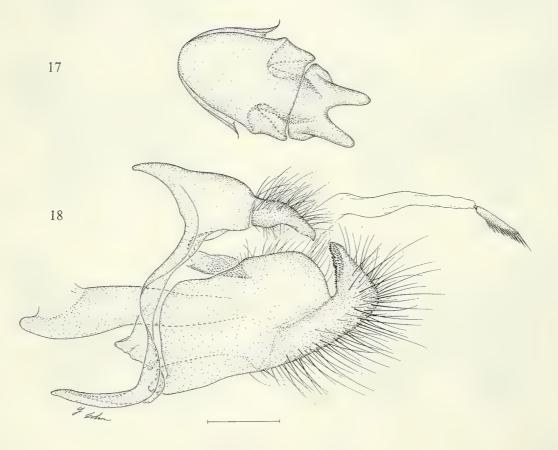
Geographic distribution. With four species on one volcano in the ACG, a pan-neotropical distribution (Mexico [Veracruz] to Bolivia), and paucity in collections, the formerly monotypic genus Venada will likely be found to contain a substantial number of species. Owing to their presumed similarity, series of specimens like those produced by the ACG bioinventory will be desirable for their detection and characterization. The present general scarcity of Venada in museums precludes much meaningful extrapolation. Genitalic dissections of a few miscellaneous specimens suggest additional species in Mexico and Guatemala, on the one hand, and Panama, on the other; but more material is needed. Venada advena was briefly described (Mabille 1889) from a single female from Chiriqui (western Panama). The scant verbal and visual portrayal of her facies does not exactly fit the facies of any of our ACG species. It seems



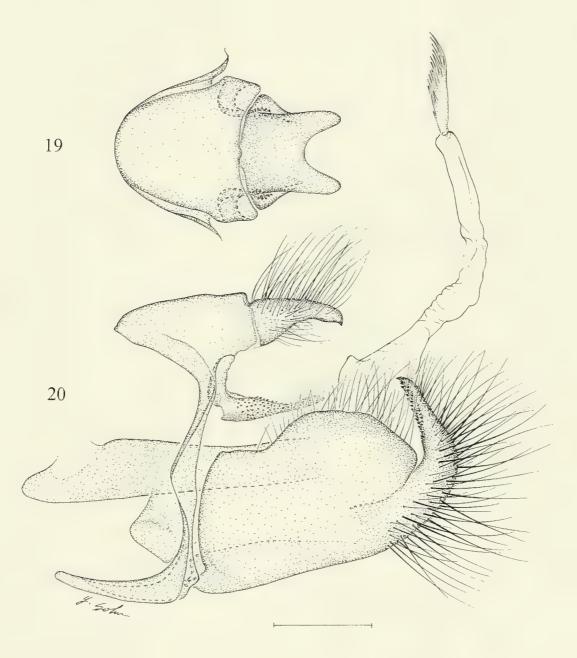
FIGS. 1–8. Adults in dorsal view (holotype males left, paratype females right) of four species of *Venada* from Volcán Cacao in the ACG, COSTA RICA (×1.4). **1**, **2**, *V. nevada*, \diamond 02-SRNP-23534, \ominus 02-SRNP-23499. **3**, **4**, *V. daneva*, \diamond 02-SRNP-20143, \ominus 01-SRNP-2550. **5**, **6**, *V. cacao*, \diamond 02-SRNP-23364, \ominus 02-SRNP-23324. **7**, **8**, *V. naranja*, \diamond 03-SRNP-4740, \ominus 01-SRNP-7133.



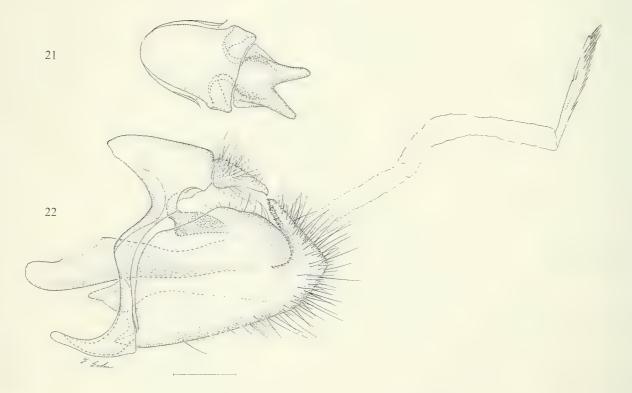
FIGS. 9–16. Adults in ventral view (holotype males left, paratype females right) of four species of *Venada* from Volcán Cacao in the ACG. COSTA RICA (×1.4). 9, 10, *V. nevada*, \diamond 02-SRNP-23534, \diamond 02-SRNP-23499. 11, 12, *V. daneva*, \diamond 02-SRNP-20143, \diamond 01-SRNP-2550. 13, 14, *V. cacao*, \diamond 02-SRNP-23364, \diamond 02-SRNP-23324. 15, 16, *V. naranja*, \diamond 03-SRNP-4740, \diamond 01-SRNP-7133.



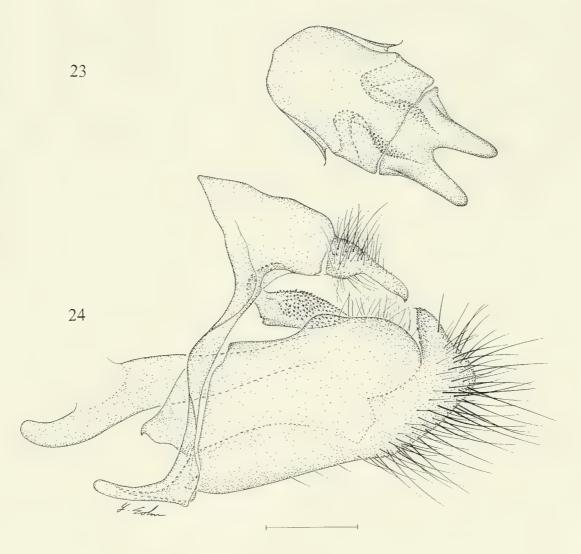
FIGS. 17, 18. Male genitalia of *Venada nevada* from Volcán Cacao in the ACG, COSTA RICA, X-5693, 02-SRNP-8926 (USNM); scale = 1.0 mm. 17, Tegumen, uncus, and gnathos in dorsal view. 18, Complete genitalia (minus right valva), with vesica everted, in left lateral view.



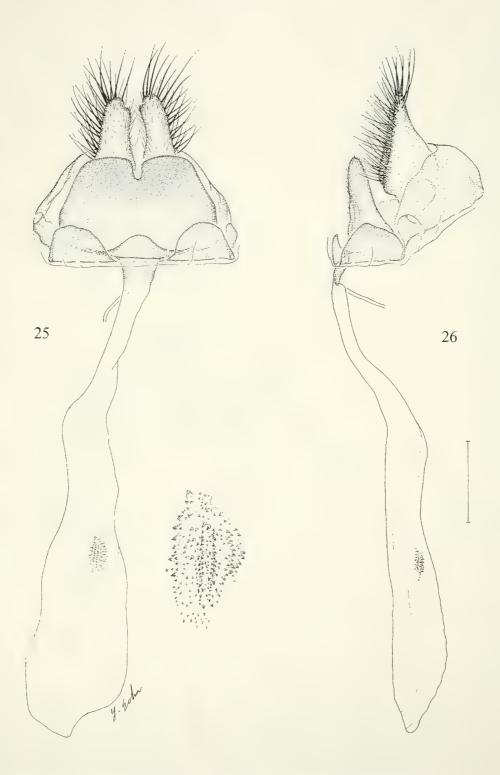
FIGS. 19, 20. Male genitalia of *Venada daneva* from Volcán Cacao in the ACG, COSTA RICA, X-5706, 03-SRNP-5862 (USNM); scale = 1.0 mm. **19**, Tegumen, uncus, and gnathos in dorsal view. **20**, Complete genitalia (minus right valva), with vesica everted, in left lateral view.



FIGS. 21, 22. Male genitalia of *Venada cacao* (holotype) from Volcán Cacao in the ACG, COSTA RICA, X-5390, 02-SRNP-23364 (USNM); scale = 1.0 mm. **21**, Tegumen, uncus, and gnathos in dorsal view. **22**, Complete genitalia (minus right valva), with vesica everted, in left lateral view.

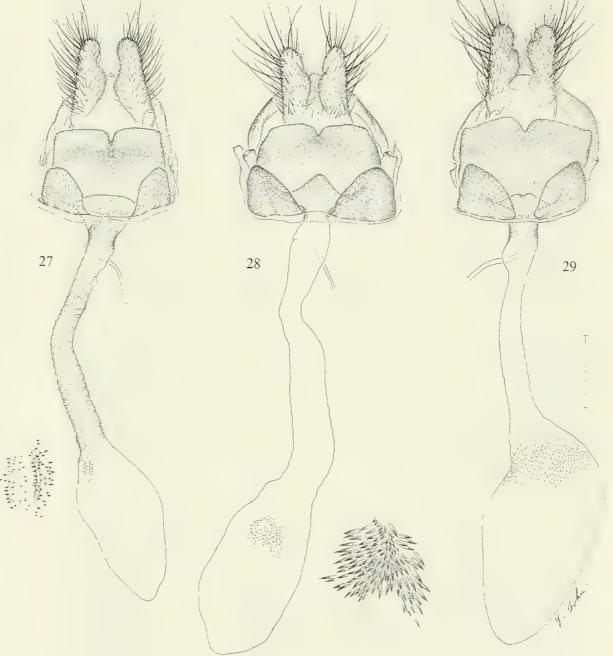


FIGS. 23, 24. Male genitalia of *Venada naranja* from Volcán Cacao in the ACG, COSTA RICA, X-5685, 02-SRNP-8086 (USNM); scale = 1.0 mm. 23, Tegumen, uncus, and gnathos in dorsal view. 24, Complete genitalia (minus right valva) in left lateral view.

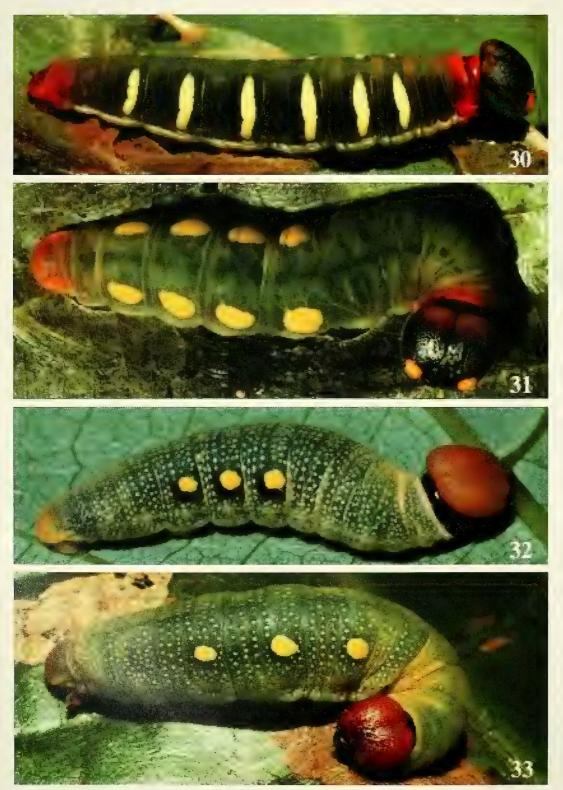


FIGS. 25, 26. Female genitalia of *Venada nevada* from Volcán Cacao in the ACG, COSTA RICA, X-4604, 97-SRNP-11146 (USNM); scale = 1.0 mm. **25**, Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view, plus enlargement of signum. **26**, The same in right lateral view.





FIGS. 27–29. Female genitalia of three species of *Venada* from Volcán Cacao in the ACG, COSTA RICA. Ovipositor lobes, sterigma, bursa copulatrix, and part of ductus seminalis in ventral view; scale = 1.0 mm. **27**, *V. daneva*, with enlargement of signum, X-5691, 03-SRNP-6535 (USNM). **28**, *V. cacao*, with enlargement of signum, X-5688, 02-SRNP-23004 (USNM). **29**, *V. naranja*, X-5687, 01-SRNP-7133 (USNM).



FIGS. 30–33. Caterpillars (last instars) of four species of *Venada* from Volcán Cacao in the ACG, COSTA RICA. **30**, *V. nevada*, 97-SRNP-11042. **31**, *V. daneva*, 98-SRNP-6010. **32**, *V. cacao*, 99-SRNP-552. **33**, *V. naranja*, 00-SRNP-9050.

closest to that of *V. daneva*, but the whitish wing fringes and ash gray palpi ascribed to *V. advena* in its original description are not evident in *V. daneva*.

What can be offered at this time is the unsurprising fact that at least three of the ACG species range more widely in Costa Rica, as shown by the following museum specimens. Venada nevada: San Vito, 1150 m, Puntarenas, 31-XII-1976, 1 \circ , G. B. Small (USNM). Venada cacao: Juan Viñas, Cartago, ?-I-?, 1 \circ (USNM); Monteverde, Puntarenas, 4 & 6-VII-1985, 1 \circ 1 \circ , W. A. Haber (USNM); Buen Amigo, San Luis, Monteverde, 1000–1350 m, Puntarenas, ?-III-1995, 1 \circ , Z. Fuentes (INBio). What appears to be Venada daneva: Rancho Quemado, Osa Peninsula, Puntarenas, ?-IV-1991, 1 \circ , J. C. Saborio (INBio).

Venada cacao also occurs in Panama. Williams and Bell (1934:132, pl. VIII, fig. 4) described and illustrated (in left lateral view) the male genitalia of "Nascus advena." The genitalia of this "Panama" male (no further data given) clearly correspond to those of V. cacao (Fig. 22).

The male of "Nascus advena" illustrated dorsally and ventrally by Godman and Salvin (1893:vol. 3, pl. 79, figs. 6, 7) is not V. advena. If it belongs to any of the ACG species of Venada, it is V. cacao. This is because the hyaline costal spots, in spaces 11 and 12 of the forewing, are two in number and are located at the upper distal corner of the large cell spot. Judging from the text (Godman & Salvin 1893:vol. 2, p. 323), this illustrated male came either from Chiriqui or from Chontales, Nicaragua.

Parasitoids. None of the 15 reared caterpillars of V. cacao has been parasitized. Only one of 55 reared caterpillars of V. naranja and six of 164 reared caterpillars of V. daneva have produced parasitoids, and these have not yet been determined. The 402 rearings of V. nevada have yielded parasitoids in just 14 cases: five are the large tachinid Chlorohystricia sp. 1, a fly that also attacks Yanguna cosyra (H. Druce) and an undescribed species of Ridens in the same cloud forest habitat on Volcán Cacao; two are the generalist tachinid *Patelloa xanthura* (Wulp), which has been reared from caterpillars of 43 species of ACG hesperiids throughout dry, rain, and cloud forest; one is an as yet unidentified tachinid from cloud forest; two are unidentified ichneumonids, one from rain forest and one from cloud forest; and four are the ichneumonid Casinaria sp. 9 from both rain and cloud forest-a wasp that, in the same habitats, also attacks Y. cosyra, Creonpyge creon (H. Druce), *Phocides nigrescens* Bell, the abovementioned undescribed Ridens, Achlyodes busirus (Cramer), A. thraso (Hübner), and A. pallida (R. Felder) (but mostly Y. cosyra and Ridens). Venada apparently lacks parasitoids that are host-specific, but occasionally supports parasitoids that live mainly on a small number of other medium-to-large, dicot-eating species of hesperiids.

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